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Soft-Bodied Fossils Are Not Simply Rotten Carcasses – Toward a Holistic Understanding of Exceptional Fossil Preservation

Exceptional Fossil Preservation Is Complex and Involves the Interplay of Numerous Biological and Geological Processes

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Exceptionally preserved fossils are the product of complex interplays of biological and geological processes including burial, autolysis and microbial decay, authigenic mineralization, diagenesis, metamorphism, and finally weathering and exhumation. Determining which tissues are preserved and how biases affect their preservation pathways is important for interpreting fossils in phylogenetic, ecological, and evolutionary frameworks. Although laboratory decay experiments reveal important aspects of fossilization, applying the results directly to the interpretation of exceptionally preserved fossils may overlook the impact of other key processes that remove or preserve morphological information. Investigations of fossils preserving non-biomineralized tissues suggest that certain structures that are decay resistant (e.g., the notochord) are rarely preserved (even where carbonaceous components survive), and decay-prone structures (e.g., nervous systems) can fossilize, albeit rarely. As we review here, decay resistance is an imperfect indicator of fossilization potential, and a suite of biological and geological processes account for the features preserved in exceptional fossils.

1. Introduction

Most of the species that ever existed are extinct, and the vast majority will never be known as fossils. This is because fossilization, even of organisms with mineralized skeletons, is a rare event and few taxa enter the sedimentary record; likewise few sedimentary sequences survive subduction, or uplift and erosion, to be sampled for fossils.^[1] The bulk of the fossil record consists of those parts of organisms that are most resistant to degradation – shells, bones, and teeth. In some cases, shelly fossil remains are so abundant that thick accumulations form entire rock units – chalk, for example, is composed of the calcium carbonate plates of unicellular eukaryotes called coccolithophores. Soft parts, in contrast, are usually lost through scavenging and decay.

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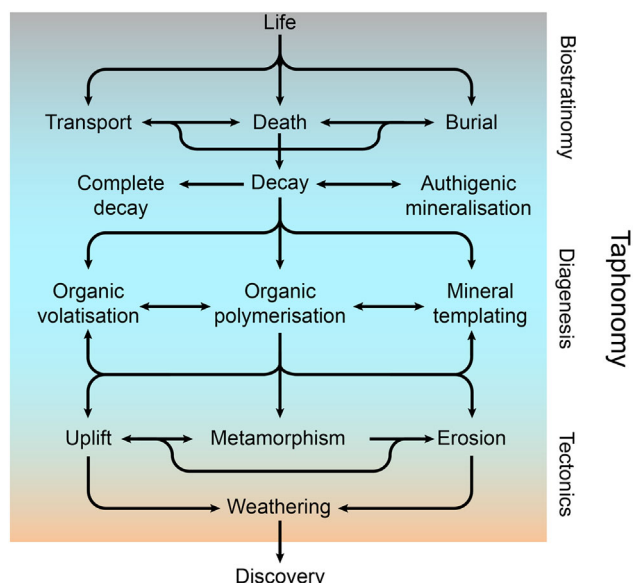


Figure 1. The long journey from live organism to fossil.

In rare cases the soft (i.e., non-biomineralized) parts of animals survive and are fossilized alongside the hard skeleton, and even wholly soft-bodied organisms (those without biomineralized tissues) can be preserved. The journey of these fossils from death to discovery involves a complex interplay of geological and biological processes (**Figure 1**) and although they are rare, they offer unique insights into the anatomy and biology of extinct life (**Figure 2**). Such “exceptional” deposits are commonly referred to as “Konservat-Lagerstätten”^[2] – a German term that is now common currency among paleontologists (Lagerstätte is borrowed from the mining industry where it means an ore deposit). Konservat-Lagerstätten occur throughout the geological record in a diversity of paleoenvironmental settings and sedimentary rock types.^[3] Soft parts of organisms can be preserved in a variety of ways: as carbonaceous compressions (**Figure 3A** and **E**); via early (authigenic) mineralization in iron sulfide (pyrite) (**Figure 2F** and **3B**) and apatite (calcium phosphate) (**Figure 2C**); and by early cementation or entombment, such as in concretions (**Figure 3D**) or within amber (**Figure 2D**). Within a single specimen, a combination of these preservational pathways can account for the preservation of the whole organism and different tissues follow particular preservational pathways. For example, **Figure 3E** shows scanning electron microscope energy dispersive x-ray (SEM-EDX) maps of a specimen of *Marrella splendens* from the Cambrian Burgess Shale of British Columbia, which preserves certain anatomical features as carbon films, pyrite, or calcium phosphate.

The Burgess Shale is one of a number of well-known examples of exceptional preservation (**Figure 3A** and **E**) which reveal diverse assemblages of early animals.^[4,5] Other examples of exceptionally preserved biotas include the plants and animals found in the Carboniferous Mazon Creek concretions of Illinois (**Figure 3D**),^[6] the fishes that preserve phosphatized subcellular details of muscle tissue in the Cretaceous Santana Formation concretions from

Brazil,^[7] and the feathered dinosaurs that reveal evidence of plumage color and flight capability from the Cretaceous Jehol sequences of north-eastern China (**Figure 2A**).^[8]

Despite the diversity of settings that yield exceptionally preserved fossils, many Konservat-Lagerstätten share biological and geological processes such as rapid burial, limited or no bioturbation, decay suppression through anoxia or euxinia, and sealing of sedimentary laminae by microbial mats and early diagenetic cements (**Figure 1**). These factors contribute to the survival of organic macromolecules^[9,10] and create the necessary microenvironments for the replication of soft tissues through authigenesis, the early precipitation of minerals.^[11] Understanding preservation (the field of taphonomy) is critical to interpreting the morphology of fossils and, in turn, their place in the tree of life and consequent significance for organismal evolution. A first step is determining which characters were originally present and which have been lost or modified by taphonomic processes.^[12] A second step involves recognizing possible homologies between features of the fossil organism and those of living taxa.^[12] The identification of homologies is essential for determining the affinity of fossils, but it is particularly challenging in cases where there is no obvious close living relative.

Rather than representing perfect snapshots of extinct organisms, soft-bodied fossils have passed through numerous filters prior to discovery that remove, modify, or preserve anatomical characters (**Figure 1**). Such processes include autolysis (self-digestion through enzymes) and microbial decay, precipitation of authigenic minerals, diagenesis (plus metamorphism in some cases), and finally weathering (**Figure 1**). The pathways travelled by exceptional fossils prior to discovery are complex, and understanding preservation is an active field of research based on investigations of fossil specimens and taphonomic experiments on extant organisms.^[13] Following discovery, further biological information can be lost or modified during excavation and preparation of a fossil; the method used to remove surrounding matrix may create artifacts and should be taken into account when analyzing important features.^[14]

A key hurdle to interpreting fossils correctly is determining which characters are missing because they were originally absent in vivo and which characters have failed to survive all of the processes involved in fossilization. Decay experiments have played a central role in interpretations of soft-bodied fossils for many years, illuminating the relative preservation potential and likely identity of different soft parts in fossils, determining the conditions required for the replication of tissues in authigenic minerals, and documenting how the molecular components of an organism are impacted by decay.^[15] More recently, however, there has emerged a tendency to apply the results of decay experiments more literally to the interpretation of soft-bodied fossils, using the relative susceptibility of morphological characters to decay as a measure of whether or not they could be preserved at all.^[16–18] While an experimental approach is important to determining how exceptional fossils are formed^[19] microbial decay is just one of many processes that can distort the original morphology of an organism. A variety of interlinked processes play a role in the preservation of different anatomical features.

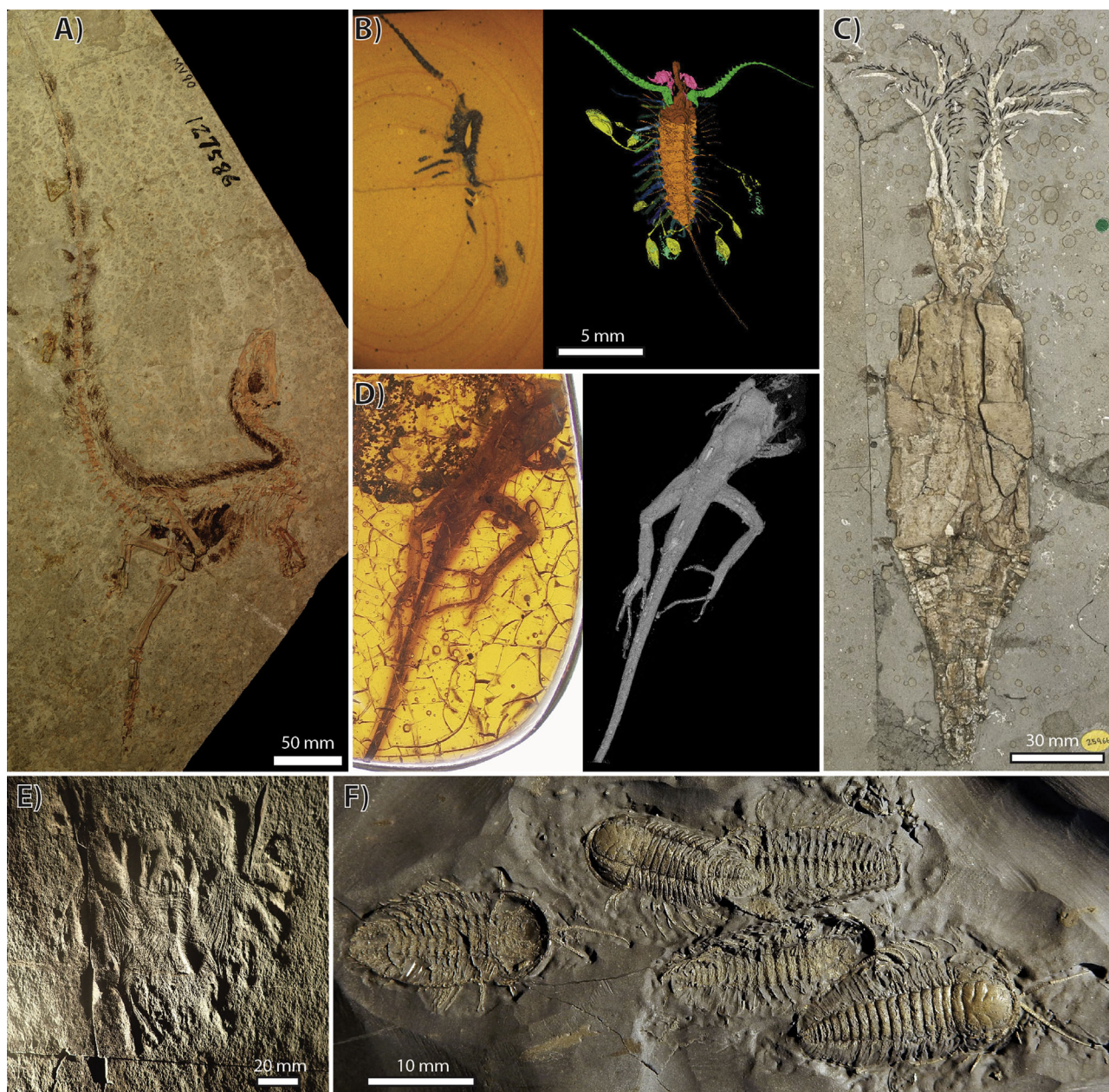


Figure 2. Exceptionally preserved fossils. A) *Sinosauropteryx prima* (NIGP 127586), a feathered dinosaur from the Cretaceous Jehol Biota preserving melanized tissues (feathers, eyes, and abdominal organs). B) *Aquilonifer spinosus* (OUMNH C.29695), a Silurian arthropod preserved in three dimensions in volcanic ash-hosted carbonate concretions from Herefordshire. Image at left shows a surface captured during serial grinding, image at right shows a three dimensional reconstruction from serial photographs.^[112] C) *Belemnitheutis antiquus* (NHMUK 25966), a Jurassic stem group decabrachian (belemnoid) from Christian Malford, Wiltshire, UK, preserving creamy colored musculature replaced by calcium phosphate and organic arm hooks. D) Fossil *Anolis* lizard preserved in Miocene Dominican amber.^[113] Image at left is a photograph of specimen, image at right shows 3D reconstruction using micro CT. E) *Haootia quadriformis*, a possible medusozoan from the Ediacaran of Newfoundland. F) Pyritised specimens of the trilobite *Triarthrus eatoni* (ROM 62891), with preserved limbs from the Late Ordovician Beecher's Trilobite Bed, New York, State. Image credits to the authors, except C (Jonathan Jackson, NHM) D (Russell Garwood and Emma Sherratt) E (Alex Liu), F (David Rudkin).

Cambrian fossils from Burgess Shale-type localities have featured most prominently in discussions of how decay determines the information preserved in exceptional fossils, because many Cambrian animals are difficult to place with confidence in a phylogeny with modern groups. The

phylogenetic position of early chordate-like fossils, for example, has attracted particular attention following the proposal of “stemward slippage.”^[20] As chordates decay, characters are lost in the opposite order to their stepwise acquisition during the evolutionary transition from the chordate stem lineage to the

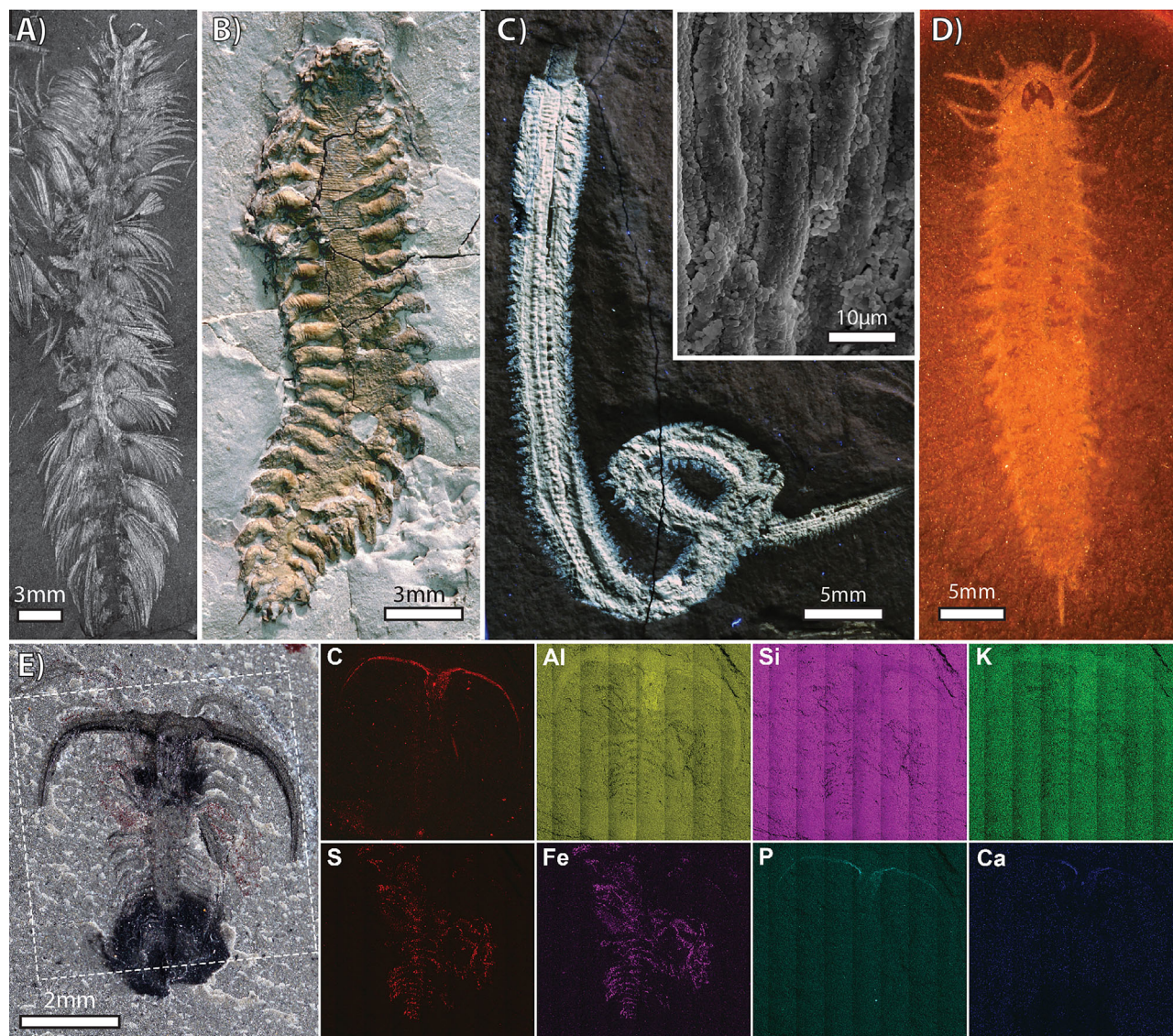


Figure 3. Same organism, different pathways of preservation. A–D show epibenthic polychaete worms preserved through different key preservational pathways. A) Preservation as a carbonaceous compression, *Canadia spinosa* (USNM 83929c), Middle Cambrian Burgess Shale of British Columbia. B) Three dimensional preservation in pyrite, *Arkonips topororum* (UMMP 73795), Devonian of Ontario. C) Three dimensional preservation of mainly muscle tissue in calcium phosphate, *Rollinschaeta myoplana* (AN 15078), Late Cretaceous, Lebanon. Inset image shows SEM photomicrograph of preserved muscle fibres. D) Entombment in an ironstone concretion, *Fossundecima konecniurum* (ROMIP 47990), Mazon Creek, Late Carboniferous, Illinois. E) Tissue specificity of taphonomic pathways in *Marrella splendens* from the Burgess Shale. Image at left shows photograph of specimen ROMIP60748. Images at right show SED-EDX elemental maps of region encompassed by the white box in the photograph where the intensity of the color indicates elemental abundance. Structures preserved as carbon films are highlighted in the C map, structures preserved by clay minerals are highlighted in the Al, Si, and K maps, pyritized structures are highlighted in the Fe and S maps and structures preserved as apatite (calcium phosphate) are highlighted in the Ca and P maps.

vertebrate crown: the farther decay progresses the more “primitive” the resultant fossil supposedly appears. Reports of organically preserved neural and circulatory^[21] tissues in Cambrian panarthropods have proved particularly controversial as an interpretation based on stages of decay^[16–18] implies that such decay-prone features should not persist and fossilize.

Here we review the diversity of processes that occur during fossilization and identify circumstances where the sequence of character loss and modification in fossils may deviate from the

null model provided by the decay of related extant animals in seawater.^[22] Clearly it is important to avoid overinterpretation of features in a soft-bodied fossil based on a simplistic comparison with the anatomy of its nearest living relative, but equally, the evidence of the fossils themselves should not be dismissed without good cause. In some cases, features that are decay-resistant do not survive diagenesis, while others that are decay-prone preserve readily. Such considerations challenge the assumption that the relative decay resistance of morphological

Box 1

The late Ediacaran (~580–541 Ma) is a unique time in earth history, predating the major radiation of the animal phyla in the Cambrian, when assemblages of macroscopic, soft-bodied organisms were preserved as high relief casts and molds, sometimes with hundreds of individuals on a bedding plane.^[29,115,116] Although most common in the Ediacaran, this taphonomic window persisted until the Devonian.^[29] Such fossils occur in a range of depositional environments, including deep marine basins, marginal marine settings, storm influenced shore faces, and shelf carbonates.^[116] Specimens may retain sub-millimetric details of mostly external, but sometimes internal,^[117] anatomy, and are sometimes three dimensionally preserved within beds.^[118] These Ediacaran organisms were buried rapidly in event beds, either by storm deposits, turbidites, volcanoclastic events, or ash falls, depending on locality.^[116] Ediacaran deposits were interpreted as census “snapshots,”^[119] but it is now recognized that they can include partially decayed individuals that died prior to the event that smothered the sea floor.^[23] The preservation of abundant in situ carcasses reflects limited or absent macrophagous scavenging during the Ediacaran.^[23] Although the mechanism that led to the preservation of these organisms remains controversial, and a single explanation may not apply to all localities, most models involve sealing the sediment. Candidates include rapidly forming pyrite crusts referred to as “death masks,”^[28,116] microbial mats,^[28] clay mineral templating^[120] and, most recently, early silicate cementation.^[29]

characters alone can be used to interpret the morphology of soft-bodied fossils.^[16]

2. The Advantages of Being Buried Alive

In order to survive the test of time, organismal remains need to be shielded from the natural processes that degrade them. Burial is common to nearly all fossils, although remains may survive on a geologically short timescale in caves or bogs, for example. The impact of burial depends on factors such as rate and type of sedimentation, availability of oxygen, and subsequent cementation and compaction. Deep burial by a single event, such as a storm, enhances the chances of exceptional preservation particularly where low levels of oxygen inhibit scavenging and destruction by macro- and micro-organisms. Carcasses typically survive on the seabed only where scavengers are absent, as in the famous Ediacaran biotas,^[23] which predate the major radiation of scavenging and macrophagous animals in the Cambrian (Box 1). Rapid burial creates a microenvironment around a carcass where bacterial activity rapidly consumes available oxygen. The anaerobic processes that follow may generate conditions that

favor the precipitation of authigenic minerals.^[24,25] Anaerobic conditions also protect organic substances from oxidation, and reactive substances, such as hydrogen sulfide, may be generated which can stabilize organic materials further (see below). Generally, the more fine grained the sediment the better the preservation of soft tissues because clay and silt limit the rate of diffusion and promote the establishment of chemical gradients around a carcass.^[26,27] Such gradients also form where a microbial mat and early diagenetic cement seal in the buried organism (Box 1): this may allow preservation in coarser sediment – even in sandstones in the case of Ediacaran assemblages.^[28,29] Sediment mineralogy, particularly of clays, may also play a role in tissue stabilization.^[13,26,30,31]

Early cementation of the surrounding sediment promotes exceptional preservation by eliminating pore space and may create a cast of soft tissue anatomy. Early precipitation of carbonate at the sediment surface^[32] or the presence of microbial mats^[33] may have promoted preservation in Burgess Shale-type deposits, for example, and microbial mats are a common feature of deposits preserving muscle tissue.^[34] In other cases, a concretion may form around a carcass, preventing collapse and promoting mineralization. The three-dimensional fossils of the Silurian Herefordshire Konservat-Lagerstätte, for example, preserve remarkable details in carbonate nodules within a volcanic ash (bentonite) which was deposited on the seafloor.^[35] Silica precipitates as chert in other settings, providing a medium for preserving carbonaceous fossils: notable examples include early prokaryotes and eukaryotes of Precambrian age,^[36] and one of the oldest terrestrial freshwater ecosystems associated with a hot siliceous spring in the Devonian Rhynie Chert of Scotland.^[37]

Flattening during and following burial is not equivalent to the squashing that characterizes road-kill, although fossils are often said to look like one. Fossils collapse as a result of decay but their outline is maintained by the confining sediment – lateral expansion due to pressure from above is not the norm. Even highly compacted vertebrate fossils which preserve soft tissue outlines show little evidence of lateral expansion.^[27,38] Flattening a fossil on a bedding plane is more like projecting a three-dimensional object onto two dimensions, as in a photograph.^[39] Specimens of the same animal buried in different orientations, such as the fossils from the Cambrian Burgess Shale (which were transported in turbulent flows), can be used to inform a three-dimensional reconstruction.^[39]

3. Decay Experiments in Sea Water Show That Information Loss is the Norm

Although fossilized muscle tissue was first recognized in a Jurassic coleoid cephalopod over 170 years ago,^[19] systematic investigation of the role of decay in the preservation of exceptional fossils has only been a major topic of research in the last few decades (for a summary of decay experiments in the literature, see Supporting Information). Earlier studies involved observations on vertebrates in natural or laboratory conditions, with little control on variables, and often took advantage of natural deaths in marine settings.^[40,41] One focus was the effect of a decaying organism on the surrounding micro-environment,

as in concretion formation.^[42] Observations of a decaying priapulid were used to interpret Burgess Shale specimens of the Cambrian priapulid *Ottoia*^[43] but it was not until the late 1980s that experiments started to explore the impact of various controls on decay.^[44,45] These early laboratory experiments showed that decay can proceed rapidly even under anoxic conditions, leading to the realization that authigenic mineralization is necessary to retain the morphology of certain decay-prone soft tissues^[45] (see Table S1, Supporting Information).

A series of decay experiments carried out in the 1990s attempted to monitor and control the complex variables involved, as well as exploring the impact of different experimental conditions on morphological decay.^[46–52] Annelids and arthropods decaying under different conditions of oxygen and temperature, for example, showed consistent patterns of morphological decay, reflecting the nature of their tissues.^[49–51,53] Interpretations of soft-bodied fossils were informed by which features were more likely to survive decay versus those that degraded rapidly.^[46,54] Observations of decay of the lancelet *Branchiostoma lanceolatum*, for example, were used to argue that the axial lines preserved along the trunk of conodonts represent the notochord, and that the apparent offset position of the conodont elements below the head reflects the decay of the supporting tissue.^[51] The same decay experiments allowed the chevron-shaped structures in *Conopiscius*, a Carboniferous chordate, to be interpreted as myomeres rather than external scales, and also indicated that a decay-resistant cuticle was not necessarily present in *Pikaia* from the Burgess Shale.^[51,55]

Decay in seawater has now been monitored in a range of taxa in laboratory experiments (see Table S1, Supporting Information): anthozoans,^[56] annelids,^[48] chaetognaths,^[57] priapulids,^[18] onychophorans,^[17] pterobranchs,^[58] enteropneusts,^[59] non-vertebrate chordates,^[20] and cyclostomes.^[60] Thus the sequence of character loss has been determined for taxa representing most clades of eumetazoans. Despite the diversity of body plans analyzed in these experiments, collectively they show that different tissues decay at different rates, with some common patterns of susceptibility to decay across different organisms, and that different character systems are lost at different stages in the decay process. Gut, muscle, and nervous tissue, for example, are among the first to decay in a broad range of taxa in decay experiments.^[17,18,48]

The majority of recent experiments were carried out in the absence of sediment in order to facilitate observations of the sequence of decay stages and to reduce the number of variables involved in the experiments. The sedimentary environment in which a carcass is buried is an important control on decay. The chemical gradients that form may stabilize organic substances or induce mineral precipitation, and the sediment supports decaying tissues and prevents the organism from disarticulating. Decay experiments that incorporate sediment reveal a role for sediment chemistry in soft-tissue preservation, where different clays, for example, may promote the preservation of some tissues but not others.^[30]

During decay experiments, certain structures persist for weeks or even months. Notable examples are the jaws and chaetae of nereid polychaetes,^[48] the notochord and myomeres of chordates,^[20] and the chitinous parts of non-arthropod

ectodermozoans such as the claws of onychophorans^[17] and scalds of priapulids.^[18] Despite the apparent decay resistance of these structures, however, they are not always preserved in fossils. The jaws of nereid polychaetes, for example, do not survive diagenesis despite being heavily sclerotized: they only survive in recent sediments,^[61] whereas the jaws of other polychaetes occur abundantly as fossils.^[62] Somewhat counterintuitively, polychaetes that mineralize their jaws are absent or rare as fossils as they are more weakly sclerotized, allowing their mineral components to disaggregate.^[61] Similarly, the notochord is absent in fossils of some members of the vertebrate crown group^[63] despite its decay resistance.

4. The Molecular Composition of Tissues and Their Decay Environment Influence Preservation Potential

Structural tissues, such as the exoskeleton of arthropods and the non-biomineralized jaws of polychaetes, are often fossilized even though when, unlike shells, they do not contain biominerals. Fossils of structural tissues encompass a broad range of taxa from across the tree of life, ranging from the cuticles of plants to the plethora of early Paleozoic “small carbonaceous fossils,” which reveal a hidden diversity of early animals, including meiofauna.^[64] These carbonaceous fossils are composed of recalcitrant biomolecules, i.e., their molecular composition protects them from decaying or breaking down rapidly and allows them to survive elevated temperatures and pressures. The collagen in notochords and the keratin in claws, feathers, and hair are decay-resistant, but do not survive geological maturation.^[65] In some cases, biomolecules may remain as biomarkers in the rock when all morphology is lost.^[10] Bond strengths, functional groups, and steric effects influence the susceptibility of different biomolecules to degradation.^[9] Nucleic acids are the least stable, followed by proteins, carbohydrates, lipids, pigments, and structural macromolecules.^[9,10] Under certain conditions, it is possible to recover more resistant biomolecules associated with fossils in a nearly intact state. Recently, for example, sterols have been reported in a 380 million-year-old Devonian crustacean preserved in a concretion^[66] and nearly intact melanin in a 200 million-year-old coleoid cephalopod.^[67] But, just as decay resistance is an incomplete guide to the preservation potential of soft tissues, in most cases carbonaceous material must undergo diagenetic modification to survive.^[68]

Labile molecules may be stabilized by reactions that occur during fossilization, including processes equivalent to tanning, caramelization, and sulfurization (vulcanization). Tannins are polyphenolic compounds with multiple hydroxyl and carboxyl groups that react with proteins and their constituent amino acids in a process similar to tanning, as in the leather industry. Tanning was invoked as an explanation of the survival of polychaete and shrimp carcasses in experiments with clays.^[30] Caramelization, well known in cooking, involves anhydrous reactions between sugars and amino acids in Maillard-type condensations to form melanoidin compounds. Melanoidins have been reported in fossil molluscs and brachiopods^[69,70] and are important in the formation of humic acids and kerogens.^[71] The reaction of proteins with saccharides to form melanoidin

complexes may also explain the preservation of skin in human bog bodies.^[72]

Sulfurized molecules are a significant component of kerogens and asphaltenes.^[73] Sulfurization involves the formation of sulfide and disulfide bridges in a manner reminiscent of the vulcanization of rubber. The preservation of bone marrow and muscles in amphibians from Miocene sulfur-rich lake deposits in Spain has been attributed to this process.^[74–76] Analyses of older fossils, complemented by maturation experiments, have shown that over time the composition of animal and plant cuticles, for example, is transformed by cross-linking reactions into more stable longer chain hydrocarbons (in situ polymerization), which incorporates lipids,^[77] a process enhanced in the presence of sulfide. This diagenetic change is time dependent, but accelerated by the elevated temperatures experienced by rocks at depth, and although it modifies the original chemical composition and internal structure of tissues, their external morphology remains largely intact.^[10]

We have a general understanding of the chemical processes involved in the fossilization of soft tissues, but the details of how preservation is affected by the composition of specific tissues and the nature of the microenvironments that develop within a buried carcass are largely unknown. Such an understanding is hampered by the need to deconstruct the extensive chemical alteration that fossilized soft tissues have undergone in order to determine the processes involved. It has been clear for some time, however, that the resistance of molecular components to microbial degradation (selective preservation) is an inadequate explanation of the survival of organic matter in sedimentary rocks and, consequently, of the fossilization of soft tissues.^[68,77]

5. Authigenic Mineralization Saves Tissues Apparently Doomed to Decay

Authigenic mineralization provides a mechanism for fossilizing decay-prone tissues before they are lost. The key pathways are (1) phosphatization, which preserve soft tissues at high fidelity, (2) pyritization, which retains less fine detail but played a critical role in a number of famous fossil Konservat-Lagerstätten, and (3) templating by clay minerals.

Features known to be preserved through phosphatization include microbes,^[78] cells and embryos with possible nuclei,^[79] guts,^[80] epidermis,^[75] and muscles.^[46,78,81,82] Experiments have revealed the importance of microbial activity in releasing phosphate and generating the necessary geochemical gradients to induce phosphatization in a decaying carcass. Sufficient calcium and phosphate ions must be available and pH must drop in order for calcium phosphate to precipitate instead of calcium carbonate (i.e., the calcium carbonate/phosphate switch).^[24] Such a decrease is a normal result of bacterial decay,^[26,31,48] but phosphatization tends to favor the preservation of particular tissues and taxa.^[81,83]

Decay experiments have shown that phosphatization occurs on a laboratory time scale and is not necessarily restricted to a few unusual settings.^[53] Microbial activity promotes decay, destroying morphological information in soft tissues, but it is also essential to establishing the conditions that lead to the replication of soft tissues in authigenic minerals.^[11,84–86] The nature of microbial

controls is subtle and poorly understood. For example, different species of the same genus of bacteria have been shown to degrade soft tissue on the one hand and replicate cellular organization and morphology on the other, providing a potential pathway for mineral replication of soft tissue features.^[19,87]

Authigenic mineralization varies with conditions and between taxa. The fidelity of preservation differs in different muscle tissue types, for example,^[81] mineralization of soft tissue is rare or absent in some taxa even where they occur in association with others that are heavily phosphatized,^[81] and some taxonomic groups are not represented in the fossil record due to taxon-specific effects during decay.^[88] The longitudinal and parapodial muscles of the Cretaceous amphinomid polychaete *Rollinschaeta myoplana* (Figure 3C) are preserved with greater fidelity than other muscle groups although muscle tissue is rarely preserved in associated polychaetes, and only with low fidelity.^[81] These differences may reflect specific properties of amphinomid muscle, such as greater density or availability of phosphate compared to other polychaetes. Circular muscle may be preserved with less fidelity than other muscle types, based on the evidence in fossil annelids,^[81] or the presence of these muscles may be uncertain due to poor preservation, as in the gilled lobopod *Pambdelurion* from Sirius Passet.^[89] The absence of phosphatized soft tissue in fossil decabrachian cephalopods has been shown experimentally to be due to the presence of ammonia for buoyancy regulation, which prevents the drop in pH necessary to allow phosphatization.^[88] An understanding of the controls on phosphatization is therefore important for constraining interpretations of authigenically mineralized soft tissues.

Authigenic mineralization can upend the sequence of character loss observed in decay experiments. In polychaetes, for example, the cuticle and chaetae persist in decay experiments for many weeks,^[48] while muscle tissue and digestive organs are readily lost. In contrast, fossil polychaetes show that complete myoanatomy may survive when conditions favor extensive phosphatization^[82] while decay-resistant cuticular features such as chaetae may be absent or poorly preserved.^[81] In extreme cases, characters that decay rapidly are preserved to the exclusion of characters that undergo little degradation on a laboratory timescale.^[81]

Pyritization, like phosphatization, although relatively rare, can preserve the original three-dimensional morphology of structures that normally decay. Examples include the appendages and eggs of trilobites and ostracods in Beecher's Trilobite Bed in the Ordovician of New York State (Figure 2F),^[25,90] the soft parts of a diversity of marine animals in the Devonian Hunsrück Slate of Germany^[91] and of the polychaete *Arkonips* from the Devonian of Ontario (Figure 3B).^[92] Pyritization of soft tissues occurs in fine-grained siliciclastic sediments that are otherwise poor in organic matter but enriched in iron.^[91] In such settings, decaying carcasses provide a locus for anaerobic sulfate reduction, resulting in the production of sulfide and formation of pyrite.^[91,93] Iron-enriched pore water is a prerequisite for pyritization, and may explain why pyrite framboids commonly occur in association with soft-bodied fossils from the Cambrian Chengjiang biota but are rare in similar Burgess Shale-type assemblages elsewhere in the world.^[93,94]

Templating by clay minerals has also been invoked as a tissue specific mineralization process responsible for preservation of organisms in the Burgess Shale.^[95] Such clay mineral templates are common in organic walled fossils (such as graptolites) in

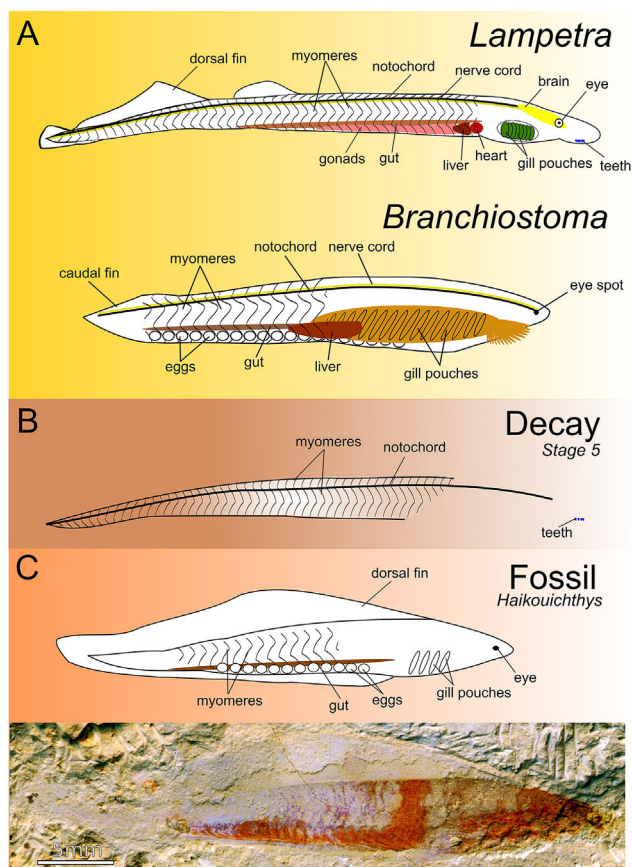


Figure 4. Characters resistant to experimental decay do not closely match characters preserved in fossils. Instead, fossils preserve a combination of decay-resistant and decay-prone characters. A) Schematic anatomy of extant lamprey (*Lampetra*) (top) and lancelet (*Branchiostoma*) (bottom). B) Reconstruction of lamprey in an advanced state of decay (decay stage 5, sensu Sansom et al.^[20]). C) Drawing (top; after Zhang and Hou^[114]) and photograph (bottom) of an exceptionally preserved fossil chordate, *Haikouichthys* Yunnan Key Laboratory of Palaeontology YKLP00195. Photograph by Peiyun Cong, Yunnan University and NHM, London.

metamorphosed fine grained siliciclastic sediments^[96] and a broad survey of Burgess Shale-type localities suggest that conservation of organic tissues is the primary mode of preservation that unites these Lagerstätten.^[94] Clay minerals have long been implicated in having a role in the processes that suppressed the breakdown of tissues in Burgess Shale type localities^[97] and experimental evidence suggests that clay mineralogy has a profound impact on tissue decay.^[13]

6. Using Decay as a Guide to Preservation Can Compromise the Interpretation of Fossils

An overemphasis on the sequence of decay observed in experiments in interpreting soft-bodied fossils assumes that the anatomy preserved is a reflection of original morphology tempered by decay loss (the “rotting away” of characters).^[16–18,57] Decay experiments on a diversity of taxa (Table S1, Supporting Information) have shown that “stemward slippage”^[20] appears to be a peculiarity of

chordates. This is perhaps not surprising as there is no a priori reason why derived characters should be more or less decay-prone than others – in arthropods, for example, morphological characters sheathed in cuticle have a high preservation potential, and cuticular characters are subject to evolutionary change at all levels in the systematic hierarchy of Arthropoda.

A too-literal interpretation of fossils as representing a stage of decay in the laboratory risks ignoring other factors that affect the loss or preservation of morphological features. Although we need to be careful not to overinterpret the anatomy of soft-bodied fossils, we cannot assume that because features decay rapidly in experiments, they can never be fossilized, particularly if the fossil evidence itself is compelling. Animals that lack an extracellular cuticle, such as the soft-bodied mollusc *Odontogriphus*,^[98] enteropneusts^[59] and the chordate *Pikaia*^[55] are preserved in the Burgess Shale, and chaetognaths are preserved in both the Burgess Shale^[99] and Chengjiang biotas.^[100] Although the body outlines of fossil chaetognaths are poorly defined,^[100] those of *Odontogriphus*, *Spartobranchus*, *Oesia*, and *Pikaia* are clearly preserved, indicating that structures that lack the extracellular materials in cuticles nonetheless survive in Burgess Shale-type deposits (*contra*^[101]). Other decay-prone characters, such as features of the digestive system, are preserved as reflective films (representing carbon) in both Sirius Passet and Burgess Shale fossils. The identification of features of the digestive system is relatively straightforward based on their position and morphology (e.g., often highly detailed anatomy preserved in midgut glands) and has caused little controversy, even though decay studies suggest that they should have a very low preservation potential.^[18] Early authigenic mineralization often confers a greater degree of three-dimensionality to fossilized guts than to more decay-resistant features, including cuticle.

6.1 Decay Induced Distortions Are Not Characteristic of Exceptional Fossils

Yang et al.^[102] identified well organized segmental ganglia in a total group euarthropod from the Chengjiang biota. Sansom^[18] argued that this interpretation was implausible based on the rapid loss of nervous system morphology in his decay experiments on priapulids. However, it is difficult to conceive how shrinkage of other anatomical features could generate the well-organized features^[103–105] and serially repeated structures^[102] interpreted as fossil nervous systems. Shrinking a cuticle would not be expected to generate a rope-ladder morphology that was the primary basis for identification as a nerve cord.

Decay experiments on priapulid worms have shown that carcasses develop pronounced asymmetrical bulges as they decay in seawater, presumably as a result of fluid and gas build up (e.g., Sansom,^[18] Figure 3 and 4). It does not necessarily follow, however, that the relative body dimensions of fossil priapulids are likewise distorted and should be excluded from phylogenetic analysis. Priapulid specimens from the Burgess Shale are approximately symmetrical even where separation of the body wall from the cuticle indicates that some decay has taken place.^[43] The familiar dark stains at the anterior and posterior of Burgess Shale fossils are

not due to compaction, but reflect the escape of decay fluids; distortion of the body shape was limited by the confining effect of the sediment. Similar considerations apply to the decay of onychophorans. Asymmetrical bulges and distortion of the body observed in experiments^[17] have not been observed in fossil lobopodians, even where the internal anatomical features have separated from the cuticle indicating that decay has taken place, such as in *Antennacanthopodia*.^[106] Lobopodian fossils typically show no evidence of distortion, suggesting that build-up of decay fluids (sometimes evidenced by dark stains) is sometimes accommodated by leakage rather than deformation of the body.

6.2 Some Decay Resistant Features Do Not Preserve in Exceptional Fossils

The claws and jaws of onychophorans are decay resistant and, on that basis, their absence in *Helenodora* from the Carboniferous Mazon Creek deposit has been argued to be primary.^[16] Likewise *Helenodora* is thought to have lacked slime papillae; they too are absent, and their preservation potential should be similar to other cuticular structures such as dermal papillae and limbs. The presence or absence of slime papillae is significant, as their presence in *Helenodora* would indicate a phylogenetic position close to the crown group of Onychophora. A recently described onychophoran from Montceau-les-Mines, France, a similar late Carboniferous assemblage preserved in concretions, preserves slime papillae and crown group-like antennal annuli, papillae, and trunk plicae but not claws.^[107] Onychophoran claws have a deep evolutionary origin evidenced by their presence in stem onychophorans (lobopodians) such as *Hallucigenia* from the Cambrian Burgess Shale.^[108] The presence of an otherwise crown onychophoran-like suite of characters without claws suggests that other mechanisms may explain their absence in both Carboniferous taxa, such as rapid shedding from the body soon after death, as observed in fossils in amber.^[109] Furthermore, the highly retractile nature of slime papillae renders them difficult to observe, even with near pristine preservation of external cuticular anatomy and the use of synchrotron tomography,^[109] so they too may also have been present in *Helenodora*, but are not preserved.

Experiments on cyclostomes and invertebrate chordates^[20,60] showed that the notochord persists until the latest stages of decay (Figure 4). Nonetheless, the notochord is apparently absent in several taxa from Mazon Creek^[63] even though other characters indicate that they belong to the vertebrate crown group, and therefore, possessed a notochord. The notochord is also absent in *Haikouichthys*, a total group vertebrate from the early Cambrian (Figure 4B), despite the preservation of characters such as eyes, gill pouches, and a dorsal fin, which disappear more rapidly in decay experiments, but clearly indicate a phylogenetic position consistent with the presence of a notochord.^[20,60,110] *Haikouichthys* preserves a chimaeric assemblage of decay-prone and decay-resistant characters rather than corresponding to a particular decay stage (Figure 4). Likewise, the notochord is poorly preserved or equivocal in *Pikaia* and *Haikouichthys*, whereas other decay-prone characters including the eyes and nasal capsules are preserved in both taxa as well as the liver and heart in *Metaspriggina*, a vertebrate

from the Burgess Shale.^[111] Explaining the characters preserved in these fossils requires an appeal to more than just simply decay resistance. Furthermore, the quality of preservation varies among individuals of the same taxon, between taxa preserved in the same bed and between fossil assemblages, demonstrating that variations in environmental parameters influence the quality of preservation at different temporal and spatial scales.^[33,81]

7. Conclusions

The fossilization of a carcass involves the interplay of rapid burial, decay, precipitation of minerals such as phosphate or pyrite, and subsequent diagenetic changes that occur on a geological time scale. Although decay experiments provide an important model for understanding the processes that impact soft-tissue preservation,^[19,22] fossils do not simply represent a stage of decay. Decay-prone tissues (e.g., muscle tissue) can be preserved by authigenic mineralization even when more decay-resistant tissues are lost. Conversely decay-resistant structures (e.g., the notochord) often do not survive longer-term alteration. The assumption that decay-resistance determines which features fossilize^[17,18] does not apply to every soft-bodied fossil. Factors other than decay can result in counterintuitive results (such as the preservation of muscle and not cuticle). Understanding and interpreting fossils requires the consideration of geological as well as biological processes; the preservational context is as critical as the evidence of the fossils themselves.

Supporting Information

Supporting Information is available from the Wiley Online Library or from the author.

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Conflict of Interest

The authors declare no conflict of interest.

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